PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Investigations into the Segmental Representation of Movements in the Lumbar Region of the Mammalian Spinal Cord. Excitation of the Spinal Cord, and Direct Excitation of the Spinal Nerve Roots

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V. *Investigations into the Segmental Representation of Movements in the Lumbar Region of the Mammalian Spinal Cord.—Excitation of the Spinal Cord, and Direct Excitation of the Spinal Nerve Roots.*

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INTRODUCTION.

THE following research was carried out in consequence of suggestions made to me by Professor VICTOR HORSLEY, to whom I wish to express my thanks for placing the facilities of his laboratory at my disposal, and for his advice and criticisms during the prosecution of the work and in the preparation of the paper. I also wish to return my best thanks to Professor JOHANNES GAD, in whose laboratory the first part of the work was carried out, for his ever-ready and constant help and advice. I have further to thank my friend Dr. RISIEN RUSSELL for his kindness in assisting me in some of my earlier experiments on the monkey.

The researches were undertaken with the view of throwing light upon the degree to which certain movements or, speaking more precisely, sensori-motor (kinæsthetic) phenomena are represented in any given segment of the lumbo-sacral region of the mammalian spinal cord, and further what relationship exists between the representation of one movement and that of another. It is clear that at least three methods suggest themselves as means whereby this problem may be attacked, *e.g.*, (1) the excitation method, (2) the method of exclusion by ablation, and (3) the so-called degeneration method. Of these Nos. (2) and (3) have been already in part employed (No. (2) SHERRINGTON, RISIEN RUSSELL, No. (3) GRÜNBAUM), but believing that with suitable precautions more exact localisation could be obtained by the excitation method, I have so far adopted that alone.

Of necessity a number of side issues of interest and importance have presented themselves, and have been considered and studied so far as was consistent with the pursuit of the general plan of the research.

In this, the first part of the work, the procedure adopted was that of exciting either root of a given segment and observing the resulting movements. Later on, as described in the second part, the segments of the cord were directly excited, and the movements evoked recorded.

Historical Introduction.

Although a series of laborious investigations have been carried out to determine the localisation of certain movements and the physiological relationship of various muscles in and to definite segments of the spinal cord by Ferrier and Yeo, Bert and Marcacci, Forgue, Sherrington, and Russell, all these were limited (controlled by exclusion experiments) to stimulation of the motor roots. I am only aware of one antecedent localisation experiment carried out by stimulation of the posterior roots. This is one by Sherrington, 'Jl. Physiol.' vol. 13, p. 730, in which he endeavoured to obtain from the posterior root the same effect which is got by excitation of the anterior root, but he came to the conclusion from this experiment that the representation of movement in the two cases did not correspond. Nor can I find any record of the direct excitation of the surface of the cord for the localisation of movement. Of course experiments on the conducting channels are not now under consideration. Inasmuch as the present research is limited to the lumbo-sacral region, it is only necessary to summarise in tabular form the localisation already obtained by excitation of the anterior roots.

Methods of Investigation and Precautions Observed.

(a) *Species of Animal.*

The animals chiefly employed were the dog and monkey (*Macacus sinicus* and *rhesus*). The rabbit was tried in a few instances, and the results obtained with it, in so far as they went, agreed with those in the dog and monkey; but the animals succumbed so easily to shock that they did not prove suitable for these experiments. The cat, however, in the cases experimented upon, answered admirably.

(b) *Anæsthetic.*

The narcotic agents used were morphia and ether. It is necessary to dwell for a moment on the general question of narcosis, considering that the whole of the question investigated involves the active condition of the spinal nerve centres.

The anæsthesia was pushed to a profound degree for the performance of the first stage of the operation, viz., exposure and division of the spinal cord. Inasmuch as the whole of the body below the section was forthwith anæsthetic and analgesic, the

necessity of deep narcosis no longer existed, and it was consequently possible to obtain the most important results with a relatively slight degree of narcosis.

Proceeding now to special considerations of the narcosis with different agents :—

1. *Morphia.* Morphia, as is well known, in moderate doses heightens reflex action aud producing analgesia. It was, therefore, a very valuable narcotic in the present research. It was invariably employed in the dog in doses of from 15 to 20 c. grm., and was given hypodermically about ten minutes before the commencement of the operation. Ether was then administered, and the animal kept at any degree of narcosis required by its means.

2. *Ether.* The employment of ether as a general narcotic was found very useful on account of the ease with which the intensity of the narcosis of the centres could be regulated. It introduces, however, a complication now well known, viz., its differential action on antagonistic groups of muscles (*e.g.*, flexors, extensors, &c., &c.). Since this differential influence is only observed where considerable doses are administered, it could not be regarded as a factor in the present investigation ; for in the large majority of experiments it was not found necessary to administer any after the section of the cord above the seat of operation. At the termination of the experiment, the animal was given an overdose of chloroform, and hence from first to last the causation of pain was entirely avoided.

Operative Procedure.

Exposure of Cord.—Division of Cord and Isolation of Segments.

The cord was exposed with due observation of well-known precautions. (For full details, see Gotch and Horsley, Phil. Trans., B., Vol. 182, 1891.)

The animal was kept warm by being placed on a hot-water tin and covered as much as possible.

In some cases, the spinal cord and roots were stimulated at first in continuity. In others, before proceeding to experiment, the spinal cord was completely divided at a distance varying from two to eight segments above the part experimented upon. For the section of the cord, the anæsthesia was profoundly pushed ; and then, by means of a sharp knife, the spinal cord was cut completely through in its sheath of dura mater, and a little amadou pressed gently into the bleeding points. In this way the hæmorrhage seemed to give little trouble. In other cases, the dura mater was first opened longitudinally, and a fine cataract knife being passed beneath the dorsal vessels, the cord was cut through, leaving them intact. This method answered extremely well.

Method of Excitation.

1. *Electrical.*

Apparatus.

A single Daniell cell was used and supplied to a Du Bois-Reymond's inductorium of the usual type, the secondary coil being generally 20 centims. from the primary. The electrodes attached to the secondary coil consisted of fine closely-approximated platinum points, usually 1 millim., rarely 2 millims. apart. The duration of excitation was as a rule momentary, and never exceeded 1–2 seconds.

(a.) *Excitation of Nerve Roots.*

The nerve roots were raised in the air, and the electrodes usually applied so that the direction of the exciting current was transverse to the nerve fibres.

(b.) *Excitation of the Spinal Cord.*

Direct electrical excitation of the surface of the spinal cord itself may, as a method of precision, not at first sight commend itself, but a brief experience, under the direction of Professor Gad, soon showed that it is a remarkably easy thing to obtain perfectly constant and accurate results, control of which is also readily effected. The surface of the cord was gently dabbed with small wool swabs (kept in warm saline solution and squeezed dry) before the electrodes were applied. The duration of excitation was always very brief, not exceeding one second, and attention was given to the minimal response. The value of the method may be estimated by a consideration of the following facts. On stimulating the surface of the spinal cord, as already mentioned, movement was always elicited in the leg on the side stimulated, when the electrode was applied to the surface of the *posterior* column, but never, as far as I was able to see, could movement be obtained by the application of this strength or even considerably greater strength of stimulus to the *lateral* or *anterior* columns when adequate precautions were taken to prevent the direct spread of the current to the neighbouring root fibres. It was easy enough to produce movement on stimulating the surface of the anterior columns if the motor fibres, which run almost vertically for several segments of the outer surface of the cord in this region, were not eliminated, but when all precautions were carefully taken, I could not convince myself that movement resulted from application of a current to the surface of the anterior or lateral columns, whereas that elicited from stimulating the posterior columns was always marked and quite definite, and merely depended in intensity upon the conditions stated below. For instance, applying the electrodes to the surface of the postero-external column in the 5th lumbar segment of the dog on the left side produced lateral flexion of the spinal column of the same side, flexion and adduction of the hip, flexion of the knee and toes, and movement in the tail (flexion

to the same side). But of the facts observed the chief was the very local effect which would be obtained by varying the point stimulated. Thus stimulation of a point 1 millim. centrally or laterally of a given point often produced an entirely different resulting movement, or no response at all, which fact is clearly of much importance in showing that with the above strength of current the restriction of the stimulus to one point must be sufficiently well obtained.

2. *Mechanical.*

As a means of controlling the observations derived from electrical excitation, mechanical stimulation was sometimes employed in examining the nerve roots, and was evoked by pinching the tissues with fine forceps. The results obtained were precisely the same.

The results obtained by direct excitation of the cord will now be grouped as follows :—

(1.) Gross localisation according to the general structure of the cord.

(2.) Minute localisation within the excitable area.

Results Obtained by Direct Excitation of the Spinal Cord (Dog).

Gross Localisation.

(a.) *Area Excitable.*

The excitable area of the surface of the cord itself is the postero-external column. Stimulation of the column of Goll as a rule produced no movement except in the lower lumbar region, where that column is either very narrow or entirely absent. Thus at about the level of the 7th lumbar nerve stimulation of the posterior column in the middle line produced movement, namely flexion of the hip, flexion of the ankle, and flexion of the toes.

It is probable that the effect is here due to the stimulus directly spreading to the fibres of the postero-external column owing to the narrowness of the intervening portion of Goll's column. As already observed, excitation of the antero-lateral column with any stimulus less than thrice that adequate for the posterior columns was without result. It seems, therefore, proper to conclude that the postero-external column can alone be considered for the purposes of minute localisation as excitable on its surface as compared with the other column of the cord.

The reason for this probably is, that the postero-external columns are made up almost entirely of the branches (ascending, descending, and collateral) of the posterior roots, and that these are at and near the surface of the cord.

(b.) *Unilaterality.*

In the large majority (91·5 per cent.) of experiments on animals, the fact was

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strikingly evident that the movements produced were limited to the side stimulated. Only in three dogs in thirty-five (8·5 per cent.) could movement be produced in both legs—*i.e.*, sides—by stimulating only one side of the spinal cord. That this double effect was not due to the direct spreading of the current to the posterior column of the other side was proved in each case by the fact that application of the electrode to a point or points nearer the middle line and at the same level produced no movement whatever. In one of the cases the same double result was obtained from stimulating one posterior column even when the spinal cord had been split completely through at the anterior and posterior fissures as far down as three segments below the point where the cord was excited. In this particular preparation the cord was transversely divided* just above the point first stimulated, and after vertical splitting the halves were drawn apart, but on then splitting the cord through another segment the double effect vanished, though the lateral effect remained. Such double effects, therefore, are attributable to (1) the commissural connections of the two halves of the cord and (2) the degree of excitability of the cord fibres in particular cases.

(c.) *Vertical Extent of the Spinal Cord in the Dog; Movement in the Lower Limb can be produced.*

In the dog movements in the lower limb can be produced from stimulation of BURDACH'S column along the following vertical extent, from the upper border of the 13th† dorsal segment to the lower border of the 1st sacral segment.

Movements.

Flexion and adduction of the hip from the upper border of the 13th dorsal segment to the lower border of the 6th lumbar segment.

Flexion of the knee from the lower border of the 1st lumbar segment to the lower border of the 7th lumbar segment.

Flexion of the ankle from the lower border of the 1st lumbar segment to the upper border of the 7th lumbar segment.

Flexion of the toes from the upper border of the 1st lumbar segment to the upper border of the 1st sacral segment.

Closure and protrusion of anus from the lower border of the 4th lumbar segment to the upper border of the 2nd sacral segment.

Movement of tail from the upper border of the 5th lumbar segment to the lower end of the sacral region.

* The description of the result obtained after dividing the cord to separate it from the higher centres is given on the next page.

† The term segment is used here in the sense given to it by Professor SCHÄFER (QUAIN'S 'Anatomy,' 10th edit., vol. 3, Part I., p. 3), namely, the portion of cord which is in anatomical relation with any given root, and which is therefore limited above and below by imaginary transverse lines, drawn arbitrarily at a point midway between the centres of attachment of adjoining roots. These imaginary lines are termed in this paper, for the sake of clearer description, the upper and lower borders respectively.

From this it will be seen that the various areas in the postero-external column, the stimulation of which on the surface of the cord produces movements in the limbs, anus, perineum, and tail, all overlap one another, but that, on the whole, the hip area is a little nearer the cerebrum than that for the toes, and the area for the knee more proximal than that for the foot, and so on; but the whole representation of the joints is so brought together within the narrow space of the lumbar enlargement that no sharp division of the points of maximal representation is possible. This much ascertained, it was necessary to still further differentiate the foci of representation of the movements resulting from direct stimulation of the cord by a control experiment.

For this purpose Professor Gad suggested the application of a fine hot needle transversely to the path to be divided, and by this means it was quite easy to cut any particular strand of fibres without pressing on surrounding points and without causing hæmorrhage of any kind. For instance, in a dog under ether and conditions as described above application of the electrodes to the postero-external column at any point of the 4th or 6th lumbar segment produced flexion of the hip and knee, and these movements seemed identical in every respect; then by gentle application of the red-hot needle the postero-external column was divided across in the centre of the 5th segment, after which stimulation of the 4th segment only evoked flexion of the hip, whereas stimulation of the 6th segment produced only flexion of the knee. This fact is of great interest, especially in relation with the observations of Ramon-y-Cajal and Barbacci, because it is so plain that movement which results from stimulation of the posterior external column must be brought about not only by means of stimulation of the short reflex arc fibres in the same segment, but also by means of stimulation of the intersegmental (see also below) fibres (Ramon-y-Cajal), and in all probability by stimulation either directly or indirectly of the collateral fibres as well.

(d.) *Effect of transversely dividing the Cord above the Lumbar Enlargement.*

It was expected, and not without reason, as the experiments detailed show, that in excitation of the uninjured spinal cord the influence of the higher (cerebral) centres could be readily and adequately abolished by the employment of ether narcosis. To render, however, the conditions more absolute towards the end of the experiment, a complete transverse section of the cord was made at a variable distance, usually from two to six segments above the part investigated, and the excitation repeated.

For this purpose the animal was placed under deeper narcosis by ether, so as to diminish shock as much as possible, and then the cord and vessels were completely divided by a sharp cataract knife, the two parts of the cord retracting so that a gap of at least 6 millims. to 10 millims. resulted. The hæmorrhage was usually sharp, but, by the application of a little amadou to the bleeding points, it almost immediately ceased and gave no further trouble. With a view to diminish the hæmorrhage and

to maintain the circulation in the cord, a cataract knife was later passed under the dorsal vessels, and then by cutting forwards the cord was left with as good a circulation as possible. This method answered very well.

The only result observed to follow such separation of the cord from the brain, upon the movement elicited as above described, was one of increased excitability. The limits described (p. 196) (areas of vertical extent) were found to prevail precisely, and the cord was excitable, quite up to the level of the section, a smaller stimulus being necessary to produce the same movements as before. For instance, the distance of the secondary from the primary coil before section of the cord being 30 millims. for an adequate stimulus, the same result was obtained after division of the cord with secondary coil 50 millims. or 60 millims. from the primary. As regards the above-described influence of section, other conditions, as is well known, exerted an obvious effect. Thus, for instance, increasing the narcosis diminished the excitability, or even removed it; and, on the other hand, repeated stimulation either of the cord or the posterior nerve roots (see below) increased the excitability.

Further, if the cord were not irrigated from time to time with saline solution or other suitable agent, but allowed to dry, then for a time its excitability was increased. Again, the application of the red-hot needles described above gave rise to an increase of excitability.

As far as was compatible with the performance of the foregoing experiments, the knee-jerks were investigated, and it was found, of course, that with the cord intact they were present, but were influenced by the conditions which increased or diminished the excitability of the cord. When the cord was cut through in the dorsal region, and it was perfectly obvious from the gap of half-an-inch or more between the two portions that no direct communication could exist between the two parts (and therefore between the lumbar region and the brain), the knee-jerks, nevertheless, persisted in nearly every instance (in some thirty animals), and were much more active and more readily elicited than before the section of the cord. Sometimes soon after section the knee-jerks could not be elicited, but by waiting a few minutes to allow the shock to diminish or pass away they could almost invariably be obtained, and that in a more active condition than before the section. These observations, it will be remembered, were made on the dog alone.

Monkey. Anterior roots.	Ferrier and Yeo, 1881, 'Proc. Roy. Soc.,' vol. 32, p. 18.	Forgue, 1883, 'Distribution des Racines dans les Muscles des membres.'	Sherrington, 1892, 'Journ. Phys.,' vol. 13, No. 6, p. 648.	Russell, 1893, 'Proc. Roy. Soc.,' vol. 54, p. 254.
1st post thoracic (lumbar).	Flank muscle only	..	Retraction of abdominal wall .	No intrinsic movement in the limb.
2nd ditto . . .	Flank muscle only	..	Retraction of abdominal wall, slight flexion of the hip.	No intrinsic movement in the limb.
3rd ditto . . .	Muscles of the flank—not of leg (0 cruris).	..	Lower part of abdominal wall, flexion of hip, slight flexion knee, slight ext. rotation thigh.	Slight flexion at the hip.
4th ditto . . .	Flexion of thigh, extension of leg—ilio psoas—partorius, adductors and extensors cruris.	Flexion of thigh, extension "de la jambe," adduction.	Contraction of lower part abd. wall, flexion and adduction of hip, slight ext. rotation of thigh.	Flexion at the hip, adduction of thigh, extension of knee.
5th ditto . . .	Extension of thigh, extension of leg, pointing of great toe, raising of outer edge of foot (= gluteal adductors, ext. cruris, peronius longus).	Ext. (not of hip) "de la jambe," adduction of thigh, dorsiflexion of ankle, inversion of sole.	Flexion of hip, adduction of thigh, extension of knee, slight flexion of ankle, slight inversion of sole, slight extension of hallux.	Extension of whole limb, adduction and int. rotation of thigh, dorsiflexion of the foot.
6th ditto (5th lumbar in man).	Ext. rotation of thigh, flexion of leg with inward rotation, plantar flexion of the foot, flexion of hallux and toes at their distal phalanges, outer edge of foot somewhat raised (= hamstrings, sural muscles, long flexors, tibialis ant. and post. peronei, and extensors of the toes).	Ext. of thigh and ext. rot., slight flexion of knee, eversion of sole, flexion of digits at "au niveau des 2nds phalanges."	Extension of hip, adduction of thigh, weak flexion or ext. of knee, flexion of ankle, inversion of sole, extension of toes, weak adduction of hallux.	Extension of hip, adduction and ext. rotation of thigh, flexion of knee with ankle at right angles and everted flexion of distal joints of hallux and digits.
7th ditto (1st sacral in man).	Flexion of the leg (hamstrings), plantar flexion of foot, abduction of the hallux, flexion of toes at proximal phalanges, flexion of toes hallux at the distal phalanges, slight ext. rotation of thigh.	Flexion of knee, extension of ankle, flexion of digits, inversion of sole.	Extension of hip, slight ext. rot. of thigh, flexion of knee, extension of ankle, eversion of sole, flexion of digits with strong adduction of hallux, depression of root of tail.	Extension of hip, flexion of knee, extension of ankle, inversion of the sole, flexion of metacarpophalangeal joint with the hallux flexed and adducted beneath the flexed digits.
8th ditto (1st sacral) (2nd sacral in man).	Adduction of flexion of hallux (basal phalanx), plain of proximal phalange of toes, slight separation and ext. of distal phalanges, tail moves to same side.	Adduction and flexion of hallux, flexion of digits (terminal phalanges), and bringing together of fingers.	Slight ext. rot. of thigh, ext. of hip, flexion of knee, strong ext. at ankle, strong flex. and add. of hallux, flex. of digits in internal position.	Interosseal flexion of the digits, flexion and adduction of the hallux.
9th ditto (2nd, 3rd, and 4th sacral).	Movements in tail only (six times experimented).	Tail only.	Slight ext. rot. thigh, flex. and add. of hallux, flex. of digits.	No movement in the limb.

Peyer, Krause (Kronenberg; and Berol brachial of rabbit). Johannes Muller and Van Deen experimented on crural plexus of frog.

	Movement elicited by excitation of posterior roots.
12th dorsal posterior . .	Flexion of the side and psoas.
13th dorsal posterior . .	Flexion of side, psoas, and slight flexion of hip (once).
1st lumbar posterior . .	Flexion of side, slight flexion of hip, contraction of hamstrings.
2nd lumbar posterior . .	Flexion of side and abdominal muscles, flexion of hip, contraction of hamstrings, dorsal flexion of ankle, flexion toes, specially 3rd and 4th, tail to same side.
3rd lumbar posterior . .	Flexion of side, flexion and adduction of hip, dorsal flexion ankle, flexion toes and tails.
4th lumbar posterior . .	Flexion of side, flexion and adduction of hip, ext. knee, hamstrings, flexion ankle, slight flexion toes and tail.
5th lumbar posterior . .	Flexion of side, tensor fasciæ latæ and rectus femoris, flexion and adduction of hip, flexion ankle, slight flexion toes and tail.
6th lumbar posterior . .	Adduction and flexion hip, hamstrings, slight extension knee, flexion ankle, and inversion of the foot and movement of tail.
7th lumbar posterior . .	Slight rotation out of femur, hamstrings, and glutei, flexion of knee, slight dorsal flexion of ankle, occasional slight ext. of ankle, flex. toes and big toe, eversion of sole of foot and movement in middle and tip of tail.
1st sacral posterior . .	Extension of ankle, flexion of toes, movement in tail.
2nd sacral posterior . .	Slight flexion toes, movement in tail.
3rd sacral posterior . .	No movement in limb, but only in tail.

Results of Experiments upon the Spinal Cord in the Monkey.

Method.

The experiments were carried out in exactly the same manner as detailed above. The monkey was anæsthetised with ether. As is well known, ether answers admirably as a narcotic with monkeys, and it is easy to regulate the depth of narcosis to any degree. Previous to dividing the spinal cord, profound narcosis was produced in order to diminish the shock as much as possible. In most cases after division of the cord, the monkey remained in a drowsy condition and required no fresh anæsthetic, but ether was always given on any indication of restlessness. The operation was performed in the usual way and as already described above. As in the case of the dog, the experiment was divided into two chief stages; the first in which the spinal cord and roots were investigated while every structure was intact, and the second in which the spinal cord or various anterior roots were divided during the progress of the experiment. The only change produced by section of the spinal cord was to increase the excitability of the cord and roots below the section.

In the spinal cord of the monkey, stimulation produced the same general results as in the dog. I could not observe any movement elicited from stimulating any part of the surface of the cord, except from that of the postero-external column; this was always easily and constantly obtained. The vertical extent of this representation of movement of the lower limb in this column was limited above by, on the average, the upper border of the 13th dorsal segment, and below by the level of attachment of the 2nd sacral root to the spinal cord. Movement occurred after a very short latent period, and took the form always of flexion and adduction of the hip, flexion of the

knee, ankle and toes, with lateral flexion of the side and rumbling of the bowels, though it depended on the position of the electrode and the strength of stimulus whether only a part or the whole of these movements resulted.

Starting above the upper limit of representation, say at the 10th dorsal segment, and then working downwards, the first movement obtained is lateral flexion of the side. The animal moves as if he had suddenly been poked in the side, the flexion of the spine being towards the side stimulated. The first movement observed in the muscles of the hip was always flexion and never extension, though adduction is not infrequently added, and occasionally rotation of the hip. This movement of the hip can be obtained on stimulating the posterior external column anywhere from the level of the 13th dorsal segment of the spinal cord, as low as the attachment of the 6th lumbar nerve. The area, stimulation of which causes flexion of the toes, extends from the 2nd lumbar segment to the upper part of the 7th lumbar segment, and the area similarly for flexion of the knee commences about half a segment lower. Rumbling in the intestine was produced occasionally by stimulation of a point, or points in the postero-external column at about the level of the 5th or 6th lumbar segment, and the similar area for causing movement in the perinæum and closure and protrusion of the anus was a little more extensive and a little lower down, whilst stimulating at any level from the 3rd lumbar to the 3rd sacral produced movement in the tail. An interesting point in connection with the latter was, that according to the position of application of the (minimal) stimulus did the base, the middle portion, or the tip of the tail move, the higher in the cord the point stimulated, the nearer to the base of the tail was the portion of tail which moved, but if the stimulus was a strong one, the whole of the tail moved. The chief movement occurred to the side in which the posterior external column had been stimulated, except occasionally in the lower part of the cord where the column of GOLL was practically or entirely absent. Stimulation in the middle line caused, usually, depression of the tail, though occasionally elevation of the tail occurred, but the more laterally was the stimulus placed on the posterior external column, the more did the tail move to that side.

Similarly with regard to the lateral extent of the areas mentioned above, whereas of course a strong stimulus caused movement in all the parts named, nevertheless in each case it was quite definite that the area for the tail was nearer the middle line than that for the hamstrings, the area for the hamstrings nearer the middle line than that for flexion of the hip, and this median of that area stimulation of which caused lateral flexion of the side. That the posterior fibres as they ascend in the cord are placed nearer the middle line than those entering the cord higher up, and so on, of course, is now well known anatomically, but the arrangement has not hitherto been demonstrated functionally, nor the fact that stimulation of certain paths or areas in the posterior external column gives definite movements in definite parts. These areas seem quite constant, and, of course, overlap one another in their vertical, if not in their lateral extent. That this is so would, of course, be anticipated from consideration of

the necessarily complex structure of such an organ as the spinal cord, and absolutely sharply-defined areas could not therefore be expected in each animal. That variations in the origin and functions of the nerve roots occur even in the same species, has been shown by the investigations of FERRIER and YEO, and especially more recently of SHERRINGTON and RUSSELL. In this latter connection the experiment, detailed at page 204, is of particular importance, for it proves that not only can there be a variation in different animals, but also in corresponding nerves of the two sides, since it was shown that a stimulus applied to the left 2nd sacral anterior root produced no visible movement whatever in the lower limb, yet the same stimulus caused invariably and obviously a distinct movement in the right digits when applied to the right 2nd sacral nerve.

As in the dog, the knee jerks were occasionally tested, and were found not only present but even exaggerated after the cord had been divided, and this agrees with the previous results obtained by SHERRINGTON and RUSSELL.

Similarly, section of the spinal cord caused the heightening of excitability as observed in the dog, and the lower portion of the cord was excitable as high as within a very narrow margin of the cord section. Stimulation of the same points also gave the same results as before section, though with regard to the posterior roots (see below) it was found that movement obtained through stimulation of any given posterior root was abolished a variable distance, usually from 1 to 3 segments, below the section, and that the more oblique the position of the posterior root in contact with the cord, as, for example, in the lower part of the cord, the greater would be the interval affected in this manner. For example, section of the spinal cord at the level of, say, the upper part of the 2nd lumbar segment abolished movement previously elicited by excitation of the 2nd posterior root and gave partial results on exciting the 3rd posterior root, whilst the effects of stimulation of the 4th posterior root was unaffected. Moreover, lower down, *e.g.*, after section of the cord at the level of the upper part of the 5th lumbar segment where the nerves enter much more obliquely, the results of excitation of the 5th and 6th posterior roots are abolished, and not merely diminished, and those elicited from the 7th may be decreased.

ON THE PRODUCTION OF MOVEMENT BY STIMULATION OF THE ANTERIOR AND POSTERIOR SPINAL ROOTS IN THE MONKEY.

The general results obtained by excitation of the spinal roots in the monkey were precisely the same as those in the dog and need not be repeated, but certain differences were observed and with any other points of importance will be more considered. First of all, the effects observed on excitation of the anterior roots of the 4th, 5th, 6th, and 7th lumbar segments agreed exactly with those obtained by Dr. RISIEN RUSSELL ('Proc. Roy. Soc.,' vol. 54).

The results obtained by stimulating the central end of the posterior roots, which gave movement in the lower limb, are given below.

TABLE of Movements Obtained by Excitation of the Anterior and Posterior Roots in the Dog.

Dog.	FORGUE, p. 53. Anterior roots.	BERT and MARCACCI. Anterior roots.	Anterior roots.	Posterior roots.
1st lumbar	..	..	No movement in lower limb	No movement in lower limb.
2nd lumbar	..	..	No movement in lower limb	Slight flexion of hip and rarely flexion of knee.
3rd lumbar	..	..	No movement in lower limb	Flexion of hip with adduction and rotation, and slight flexion of knee and of the toes.
4th lumbar	Flexion of hip Adduction of thigh.	Flexion of hip	Slight extension of the hip Extension of the knee. „ „ ankle. „ „ toes.	Flexion of the hip. „ „ knee. „ „ ankle. „ „ toes.
5th lumbar	Extension of knee with adduction.	Ext. of knee (BERT) „ hip (MARCACCI)	Extension of the hip with slight adduction. Extension of the knee. „ „ ankle. „ „ toes.	Flexion and adduction of the hip. „ of the knee. „ „ toes. Lateral flexion of the tail.
6th lumbar	Femoral part of biceps producing ext. of knee with adduction.	Femoral part of biceps Producing ext. of knee.	Extension of the hip „ „ knee. „ „ ankle. „ with spreading out of the toes.	Slight flexion and adduction of hip. „ of the knee. „ „ aukle. „ „ toes. Lateral flexion of the tail.
7th lumbar	"Fessiers" (?) hamstrings. Flexion of knee. Extension of thigh (p. 54). Extension 'des orteils' of big toes.	Flexion of knee Extension of thigh.	Extension of the hip. Usually „ „ knee. Occasionally flexion of the knee. Extension of the ankle. Usually extension with spreading out of toes. Occasionally flexion of the toes with or without spreading out. No movement in tail.	Slight flexion of the hip. „ „ knee. „ „ ankle. „ and occasional spreading out of the toes. Lateral flexion of the tail.
1st sacral	No movement in tail Action of peronei. Strong flexion of big toe.	Tail only	Slight extension of the hip Flexion of the knee. Extension with rotation out of the ankle. Usually flexion of the toes. Movement of base of tail and of the anal region.	Flexion of the knee. Extension (rarely flexion) of the ankle. Flexion of the toes. Movements in the tail, perineum, &c.
2nd sacral	Tail	..	No movement in lower limb Lateral movements in tail (specially the hip) and rectum.	Slight flexion of the knee and of the toes. Tail strongly, chiefly at the base and downwards protrusion of anus.

The great difference between these results and those obtained in the dog are that the diagrammatic contrast, so to speak, between the powerful extension at all joints of the lower limb obtained by stimulating the 5th, 6th, or 7th anterior lumbar root in the dog and the slower, yet marked, flexion at all joints obtained by stimulating the 5th, 6th, or 7th posterior lumbar roots in the dog is not obtained. In the monkey, results obtained by stimulating the *anterior* roots are complex, extension of some joints and flexion of others in varying degrees, both quantitative and qualitative, according to the root stimulated, being observed, and there is not the invariable extension characteristic of the dog.

The movements produced by stimulating the posterior roots are, of course, resultant effects, but with the exception of an occasional slight extension of the ankle or knee, according to the root stimulated, the main effect is that the bulk of the movement produced is that of flexion, in this case agreeing with that observed in the dog. Another interesting fact noted in the monkey was that, whereas by direct stimulation only the 3rd lumbar to the 1st sacral anterior root inclusive produces movement in the lower limb (RUSSELL, and the present experiments), direct stimulation of the posterior roots from the 12th dorsal to the 2nd sacral inclusive produced movement in the lower limb. From the latter fact it follows that the path for the sensori-motor reflex impulses in the cord must be both upwards and downwards, but this does not, of course, negative the general truth of the conclusion drawn from the experiments on the dog, namely, that for reasons (see above and below) the bulk of the impulses pass downwards.

A point arose in one experiment, which may seem to explain in part, or entirely, the difference in results obtained by previous observers, and notably that of SHERRINGTON and RUSSELL.

SHERRINGTON (*loc. cit.*) found that direct stimulation of the 2nd sacral anterior root produced movement in the toes; RUSSELL, on the other hand, proceeding with the greatest possible care and attention, failed in every instance to observe any movement in the lower limb under the same conditions. Stimulating in one case the 7th posterior lumbar root, I obtained movements as before described, but after gradually cutting the anterior roots from the 3rd lumbar downwards to the 1st sacral inclusive, all movement disappeared in the lower limb, though movements resulted in the tail and in the side in a most active manner, whereas, on performing the same experiment on the other (right) side, I was surprised to find that after section of the same anterior roots stimulation of the 7th posterior lumbar still evoked movement in the lower limb on that side, viz., slight extension of ankle, very slight flexion of the toes (as well as strong movement in the tail and in the side).

After careful investigation to see that no mistake had been made, I then cut through the right 2nd sacral anterior root, when neither from the 7th nor from any posterior root could I obtain movement in the lower limb. This seems to prove to me what one would expect on other grounds, viz., that the spinal cord in mammals is so

complicated in structure and functions that slight varieties are to be expected in different members of the same series, or even, as in this case, there may be a difference in the two sides of the same body Of interest is the effect of dividing various roots and noticing the change in the resultant movement elicited by stimulating a certain posterior root. This could be done in so many ways and with so many nerve roots that it is not necessary here to give more than the general conclusions to which they lead. One or two experiments, however, may be of interest.

For instance, in one case stimulation of the 5th posterior lumbar root gave lateral movement of the side, contraction in the sartorius and hamstrings. The 5th anterior lumbar root was then divided, when from the posterior root, stimulated as before, movement in the gastrocnemius was added. That is, there ensued not only no diminution in the resultant movement, but a slight increase in another direction, as if part of the stimulus passing through the posterior root were prevented from passing out along all its normal paths, and, therefore, overflowed into another channel and gave an added effect.

The 4th lumbar anterior root was then divided in the same side, when, the 5th posterior root being stimulated as before, flexion of the side, contraction of the sartorius, and extension in the knee resulted, this last being an additional new movement.

Again, in another case, stimulation of the 7th posterior lumbar root gave flexion of the hip, slight extension of the knee, dorsal flexion of the foot, and inversion of the sole, whereas after division of the 7th anterior lumbar root excitation of the posterior root gave flexion of the hip, contraction of the hamstrings, extension of the knee, dorsal flexion of the ankle, strong flexion of the toes, and inversion of the sole, *i.e.*, again an addition of new movements.

Following this up, the 7th anterior lumbar root was next divided, after which stimulation of the 7th posterior root gave adduction of the hip, contraction of the hamstrings, extension of the ankle, flexion of the proximal joints of the toes, and extension of the distal joints, and movement in the side and tail.

After division, at intervals, of the 5th, 4th, and 3rd anterior lumbar roots no further difference in the movements resulting from stimulation of the 7th posterior root could be observed. But on dividing the 1st sacral anterior root, stimulation of the 7th posterior root gave only slight extension of the ankle, very slight flexion of toes, and movement in the tail and side, and finally, after dividing the 2nd sacral anterior root, excitation of the 7th posterior root evoked movement in the tail and side only.

Minute Localization within the Excitable Area.

In addition to the vertical distribution of the representation of movements in the lumbar enlargement (postero-external column) it was found that a minute differentiation could be made out in the lateral arrangement of the fibres in the column itself. Thus, in all the lumbar segments the following arrangement prevails:—

Repeatedly it was found that with a minimal stimulus it was possible to evoke movement either in the tail (and anus) only, or in the hamstrings, or in the hip, or in the side only, and whenever this was obtained, it was an invariable rule that the point for producing movement in the tail was placed in the cord mesially of that point stimulation of which gave movement in the hamstrings, and that this latter point was mesial of that for the hip, while most external of all was the point from which movement of the side of the trunk was elicited. Of course, if the strength of the stimulus were increased, then the current spread, and stimulating neighbouring points of excitability produced concurrent movement in two or more of above-mentioned parts, such as tail and knee.

This lateral arrangement has been in part foreshadowed by the observations of MOTT on the relation between the coccygeal nerves and GOLL'S column.

The movements resulting from excitation of a segment of the spinal cord in the lumbo-sacral region and those from excitation of the corresponding posterior root are similar, but are never quite identical. In each case flexion is the predominant effect, but in the former case the resulting movements are always stronger than in the latter, and frequently movements in other parts (tail, perineum, &c.) are added. This difference is to be expected, because, of course, in excitation of the postero-external column branches and fibres (ascending, descending, and collateral) many posterior roots are stimulated.

INVESTIGATION INTO THE SEGMENTAL REPRESENTATION OF THE CORD BY COMPARISON OF THE RESULTS OF EXCITATION OF THE ANTERIOR AND POSTERIOR ROOTS.

On pp. 199 and 201 is already given in tabular form the results obtained by different observers who have investigated this subject by stimulating the anterior roots.

The prevailing notion concerning the physiological function of representation of movement in the spinal cord is certainly that the fibres along which the stimulus passes when the posterior roots are excited, are short arc fibres, *i.e.*, limited horizontally to the segment they enter.

This simple view, however, is not borne out by the results of my experiments, as will be seen by the following account.

It was soon found that there were two sets of facts giving evidence of a different kind which showed (1) that the arrangement of the centres and their afferent fibres was more complex, and (2) that some change could be brought about within the centres by stimulation of the posterior roots which affected the excitability of the anterior roots.

(a.) *Character of Movement Elicited from the Respective Roots.*

There is a marked difference in the kind of contraction of the muscle, that from the anterior root being sharp, and that from the posterior root being more slowly developed.

(b.) *Kind of Movement Obtained from the Respective Roots.*

The most striking result, however, among these general considerations was the difference in effect obtained by excitation with the same stimulus, and under precisely the same conditions, and within a few seconds of each other, of the peripheral end of the anterior and the central end of the posterior root respectively.

It was then found that, whereas stimulation of the central end of the posterior root gave flexion of the whole limb, excitation of the peripheral end of the corresponding anterior root gave extension of the whole limb. Of course throughout these experiments there has been no excitation of the cerebral end of the anterior root, except when the nerve was stimulated in continuity. Besides the fact that the whole doctrine of recurrent sensibility, as originally formulated by MAJENDIE, BERNARD, and others, does not find much support at the present time, there is also the direct experimental evidence of GOTCH and HORSLEY to show that stimulation of the cerebral end of the anterior root has no appreciable physiological effect on either the centres or channels in the spinal cord ('Phil. Trans.,' B, 1891), for these observers found that, whereas excitation of the central end of the posterior root gave maximal evidences of change in the electrical state of the spinal cord, on the other hand excitation of the central end of the anterior root not only produced no effect in the state of the spinal cord, but even stimulation of the central end of the whole of the anterior roots represented in the sciatic nerve gave, when the corresponding posterior roots were cut, no resulting change in the spinal cord whatever.

This remarkable functional distinction between the roots (viz., anterior, extension; posterior, flexion) was quite constant, and was obtained in every animal in which the experiment was made. Of course the movement which took place was a resultant effect, and was produced by the contraction of many muscles, each of which was concerned in producing either the flexion or extension of a particular joint, in one case acting with a combination of muscles when flexion resulted, and in the other case with another set of muscles when extension resulted. Hence stimulation of either of the anterior 5th, 6th, or 7th lumbar roots produces extension, and similarly that of the corresponding posterior roots flexion. So that in a sense the anterior and posterior roots appear to be antagonistic to one another in their action. Further, with spinal cord and nerves intact, stimulation of a posterior root (say the 5th) produces flexion of a joint, even when all the neighbouring anterior roots are divided. Hence this effect can only be due to the stimulus passing from the posterior root through the spinal cord along a particular anterior root to the muscles (differentiation of function in the nerve centres of that root), yet stimulation of this same anterior root produces extension. And this agrees entirely with the results obtained in a different way by Dr. RISIEN RUSSELL ('Phil. Trans.,' B, 1893).

The above experiment also goes to show that stimulation of one posterior root causes impulses to pass out along many anterior roots.

For the particular function with which we are now concerned (sensori-motor reflex) it seems certain that the path along which the impulses pass, as evidenced by movement elicited in stimulating a certain posterior root, is directed towards a point below the level of that posterior root, and not, as we might suppose, chiefly in the same segment, or even above the level at which the posterior root ioins the cord. The proof of this new conclusion is afforded by the following facts :—

Stimulation of the 3rd posterior lumbar root in the dog produces slow, but distinct, flexion and adduction of the hip and flexion of the knee ; yet stimulation of the corresponding anterior or 3rd root, so far as I was able to observe in the thirty-five dogs experimented on, never produced movement in the lower limb ; and this is all the more remarkable because a small branch is given off from the 3rd anterior root or nerve to the 4th anterior nerve, which latter supplies directly various muscles of the lower limb. Also stimulation of the 2nd anterior lumbar roots gave no movement in the lower limb, as one would expect ; yet stimulation of the 2nd posterior lumbar root gave always distinct slight flexion of the hip and knee. Thus certainly for this segment it is clear that the posterior root is in relation with efferent paths at least two segments below its attachment to the cord.

Again, if, in stimulating any given posterior lumbar root, movement resulted in the lower limb, one or more of the anterior lumbar roots were then divided in various sequences, with the result that certain differences of movement could be observed. For instance, in one experiment excitation of the 6th posterior lumbar root gave flexion of the hip, knee, ankle, and toes, contraction of the dorsal muscles of the spine, and lateral movement in the tail to the same side ; then, on dividing the anterior root of the 4th, of the 5th, and of the 6th lumbar nerves successively, the movements still obtained on the excitation of the 6th lumbar posterior root were apparently exactly the same as before the section of the anterior roots. The same fact was borne out by the following experiment in the opposite direction, viz., by dividing the roots from below upwards. In this experiment excitation of the 5th posterior lumbar root gave flexion of the hip, knee, ankle, and toes, and contraction of the dorsal muscles of the spine. The 1st sacral anterior root was then divided, and on stimulating the 5th posterior root as before the movements resulting were flexion of the hip and knee and dorsal muscles, but the flexion of the ankle was less than before, and the flexion of the toes was obliterated. The 7th anterior lumbar root was then divided, and the 5th posterior root stimulated as before, giving the result of flexion of the hip and the knee and of the dorsal muscles of the spine, but no movement in the ankle, or, of course, in the toes. In order to completely exclude the possibility of any efferent effects passing through the 2nd sacral—although my observations on the 2nd sacral anterior root accorded with those previously obtained by Dr. Russell, showing that it has no functional relationship to the lower limb—it was next divided. The movement obtained by stimulating the 5th posterior still showed no change. The 6th anterior root was next divided. Excitation of

the 5th posterior root, as before, now evolved only contraction in the back muscles and very slight flexion of the hip. The 5th anterior root was then divided, and stimulation of the 5th posterior lumbar root gave contraction in the back muscles as before, but no movement whatever in the lower limb. Of course, excitation of the 4th anterior lumbar root, on being stimulated directly, gave the ordinary result, viz., extension of the hip and knee, ankle, and toes, with spreading out of the latter.

By varying several other experiments of the same kind, precisely similar results were obtained.

From the foregoing results obtained by the excitation method, it may be justly concluded that the normal relationship of any given posterior root (sensori-motor reflex) to the segments in the spinal cord is that the destination of its root-fibres is nerve centres in segments below the point of entry into the spinal cord. It now remains to see how far this generalisation is justified by other facts obtained in other ways.

In the first place, the fact is of much interest that as long ago as 1847 CLAUDE BERNARD found that the 6th and 7th posterior lumbar roots supplied the 7th anterior root. Another point in the same direction is the fact that if the lumbar region be cut across, then stimulation of the posterior external column, as high as the margin of the cut surface of the lower portion, will give as intense a movement as before section.

Finally, the fact that all observers are agreed that, by the method of excitation of the anterior roots, the highest segment in the spinal cord from which movements have been elicited in the lower limb is the second. The experiments in the present investigation show that excitation of the cord as high as the 13th dorsal posterior segment evokes movements in the lower limb. This apparent discrepancy is, it will be seen, a proof of the position just advanced, since it shows that the uppermost nerve centre containing motor representation of the lower limb received afferent impulses by means of the posterior root, which is two or three segments higher (nearer the cerebrum). Evidence of a like kind is afforded by anatomical researches.

In the first place, SCHULTZE found that after damage to the cervical enlargement a comma-shaped area of descending degeneration occurred in the posterior columns. BARBACCI found also after a transverse lesion of the cord that scattered descending degeneration could be found throughout the whole breadth of the posterior column.

The most important anatomical fact, however, is the well-known discovery by RAMON-Y-CAJAL, confirmed by KÖLLIKER, RETZIUS, and GOLGI, that the posterior root fibres divide almost immediately upon their entrance into the cord into two main branches, one ascending and one descending. I venture to provisionally suggest that the ascending branch is, perhaps, chiefly concerned with sensory (*i.e.*, cerebral) impulses, and the lower branch with local sensori-motor reflex actions.

It has also been shown in the horse that there is a difference in level between the

sensory and motor nerves which supply the sternomastoid muscle, the sensory nerve being two or three segments higher. It is very noteworthy also that the same antero-posterior relationship of sensory and motor nerves also prevails largely in the cranial nerves.

Summary and Conclusion.

1. *Relationship of Posterior Roots to Reflex Kinæsthetic Centres.*

It appears from the foregoing experiments to be definitely established that any reflex centre derives its chief afferent impulses from a nerve root which enters the cord as a rule about two segments higher, *i.e.*, on the cephalic side.

This generalisation, established by the method of excitation, is confirmed by anatomical and pathological observations.

2. *Lateral Arrangement of Fibres in* Burdach's *Column.*

The fibres of the postero-external column are arranged in a definite and constant order from within outward, the innermost fibres (*i.e.*, those nearest the middle line) representing the most distal portions of the tail and lower limb, and the outermost the proximal.

3. Whereas direct excitation of the anterior roots in the dog produces as a resultant movement extension of the lower limb, the resultant movement produced from the reflex kinæsthetic centres of excitation of the posterior roots is always flexion. In the monkey there is not this apparent antagonism, because stimulation of the anterior roots in that animal brings out a differentiation of flexion and extension, although excitation of the posterior root gives flexion alone.

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